

DEFENDED HUNTING TERRITORIES AND HUNTING
BEHAVIOR OF FEMALES OF *PHILANTHUS GIBBOSUS*
(HYMENOPTERA: SPHECIDAE)

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Abstract.—Females of the solitary wasp *Philanthus gibbosus* (F.) defend hunting territories around the particular halictine bee nests they hunt at, against conspecific females. Halictine bee prey may be taken from within the nest or outside the bee nest when bees leave or return to their nests.

Among birds, the females of most species have no territories of their own, rather they adopt the territory of their mate and aid in the defense of his territory. Also rare are birds which defend territories solely around specific food sources such as the hummingbird which may abandon a flowery shrub, which it had previously defended, when the blossoms fall. Thus territory is abandoned when food supply fails (Klopfer, 1969). As described in the present study, females of the digger wasp, *Philanthus gibbosus* (Fabricius), are at present apparently unique among hymenoptera, if not territorial organisms in general, in defending individual territories about the future food supply of their young from conspecific females.

While the life history and behavior of *P. gibbosus* is in general better known than any other species of the genus, there are still many major gaps in our knowledge. Reinhard (1924) reported halictid bee prey being taken at flowers, and Alcock (1974) obtained indirect evidence of such hunting by observing females flying from flower to flower and in one case noted a female carrying a halictid and a tufted dandelion seed which he believed indicated the capture was made on a flower. In other areas he observed bees taken at a large halictid colony. Peckham and Peckham (1905) reported that the wasps took guard bees indicating that captures also occur near or on the ground; Evans and Lin (1959) observed one female of *P. gibbosus*, in the course of 10 minutes, enter the nest of an unidentified halictine bee four times and each time came out with a bee she took to her own nest. The most common prey species they noted was *Lasioglossum zephyrum* (Smith), there being 15 specimens. *Augochlora pura* (Say) was one of the least common species, there being three specimens. They conducted their study in Ithaca, New York. Barrows and Snyder (1973) studied the contents of 15 cells provisioned by *Philanthus gibbosus* in a vertical bank containing nest aggregations of *Lasioglossum zephyrum* located in Douglas County, Kansas. They found that eight species of halictine bees were used and *L. zephyrum* was one of the three species represented by only one specimen. This in contrast with the 53 specimens of *Augochlora pura*, the most

commonly encountered species. They concluded that the wasp did not hunt near their nest and did not enter *Lasioglossum zephyrum* burrows to capture prey. They further suggested that perhaps *Philanthus gibbosus* hunts primarily around flowers as do *P. triangulum* (Fabricius) (Tinbergen, 1932) *P. politus* Say (Evans and Lin, 1959) and *P. bicinctus* (Mickel) (Armitage, 1965).

Alcock (1974) studied an aggregation of *P. crabroniformis* Smith in a lot in Seattle, Washington. A smaller aggregation of *P. gibbosus* was interspersed in this aggregation. He reported that *P. crabroniformis* primarily captured bees by striking them in flight as they returned to their nest, and he placed his major emphasis on this method of bee capture which has not previously been investigated in *P. gibbosus* and is unknown in the literature of *P. gibbosus*.

General Characteristics of Hunting Behavior

Hunting behavior of *P. gibbosus* was studied intensively during the active season in the vicinity of a vertical sandbank in which numbers of both wasps and an unidentified halictine bee nested in number. On 30 August between 10:54 AM and 5:36 PM observations were made, barring a few absences of usually less than an hour, of the attacks by wasps on the 8 marked, and by far most frequently attacked bee nests (A to H) on the sandhill. Not all attacks were observed due to the temporary absences and since observations on other aspects of behavior were being studied simultaneously. However the representation is an accurate one since similar observations were made all summer during the active season of the wasp. The only failing is that on this particular date the wasps were unsuccessful in capturing even a single bee. However all attacks were made at the nest entrance whether guarded or not, and wasps, frequently unsuccessful at one nest, went from nest to nest and occasionally a wasp entered an unguarded nest and withdrew without prey. Experience has shown that by far the most successful attacks are made against bees assuming flight in leaving their nests or on their return to their nests, attacks not observed to occur on this date. However in the past bees were observed being taken from within the nest. A total of 63 attacks were observed to have been made at the entrance of bee nests, whether guarded or not. In attacking, wasps palpitate the head of the guard or the empty nest entrance with their antenna; and when the guard blocks the entrance with its abdomen, wasps have been observed attempting to grasp the bee by the abdomen with their mandibles and to pull it out. They also on occasion vigorously engage in biting away at the walls of the guarded nest entrance in attempts to gain entry. There were four distinct episodes in which wasps entered an unguarded bee nest. All occurred in nest A which had the largest entrance of all 8 nests. In one case a wasp entered nest A six times, each time coming

out in seconds. The same was repeated two times by presumably another wasp.

On 25 September a rather large halictine bee was caught in midflight by a female *P. gibbosus*. The bee was caught in the vicinity of the bee nest area where other bees were hovering in flight. On capture the pair fell approximately six inches to the slope below and the wasp was seen to have its sting pushed up against the bee and definitely appeared to sting the bee. The wasp then picked up the bee and flew approximately 7 feet to enter its nest in the slope. Another mid-air attempt at capture by another wasp failed and the bee then took evasive zig-zag flight. Such unsuccessful mid-air capture is a common occurrence.

On 3 September a female *P. gibbosus* was on the slope, and a number of halictine bees were flying around. One bee flew near the wasp approximately 4 inches over the ground. The wasp pounced on the bee, malaxated it and brought the tip of her abdomen up to it in what was a probable stinging effort; and in about three seconds flew off with the bee. On 3 September in another instance a halictine bee flew about 2 inches over the slope and a *P. gibbosus* flew up and pounced on her and the two fell, locked together, to the slope and rolled down the slope for approximately 4 inches; and after about 4 seconds from the time of capture, the wasp flew off with the bee. The wasp did appear to malaxite the bee and also I believe it had the tip of its abdomen in probable stinging behavior pressed against the bee. On 28 August a number of successful captures of guards were made at nest A, the nest with the largest entrance which permitted the entry of all but the larger female wasps.

A wasp probed at a halictine bee nest entrance and palpated the head of the guard with her antennae. The guard turned to block the entrance with her abdomen and the wasp soon left. Another wasp suddenly grabbed a small bee on the outside of her nest and seemed to malaxite it approximately 10 seconds and to fly off with it; and though it had curved its abdomen up to the stinging position, it appeared that it did not actually sting the bee. A few minutes later a wasp was seen to enter nest A. The female *P. gibbosus* was small enough to enter. This is only one case of the individual differences in hunting techniques among female *P. gibbosus*. Others involved waiting for returning bees at their nests, pouncing at bees leaving their nests, making mid-air captures and hunting at flowers or elsewhere as an individual habit. The territories, to be discussed, briefly mention that individual wasps have favorite nests around which they hunt. A wasp entered nest A, and a minute later a wasp entered the same nest and squeezed approximately half way in and pulled a guard out and seemed to malaxite it a few seconds and then immediately flew off with it. I definitely believe this bee was not stung. This nest immediately had a new guard in its absence. In a few minutes a wasp entered nest A and in seconds pulled out a bee, malaxated it a few seconds and flew

with it to its nearby nest in the same sand slope. Immediate stinging in *P. gibbosus* is often far from the rule. I have, on a number of occasions, caused a wasp to drop a bee she was carrying in flight to her nest; and, on being dropped, the bee proved to be uninjured, recovered and flew away.

General Characteristics of Hunting Territories

Females in flight over their vertical bank hunting and nesting area behave entirely differently toward other females below in the area in comparison to females located below them in the nesting aggregation of an open field in Brooklyn where the nests of bees are not close by their prey nests. A female coming on another female even as much as 2 feet away and the latter at a bee nest on the slope of her hunting area pounces upon the latter and either chases her off or they both fly off or the pouncer flies off. The latter much in the manner of territorial male cicada killer wasps perching in their territory being pounced on by rival males and almost invariably pursuing the rival male which pounced on the owner (Lin, 1963) or the same may be observed among territorial males of *Polistes exclamans* Viereck (Lin, 1972). Females even pursue other females in the air. The following instance represents a case seemingly identical to two territorial male cicada killer wasps which, both being over their own territory, fly aggressively at each other and grapple (Lin, 1963). Two females engaged in hunting behavior were flying inches over the slope and after about 5 seconds came close to each other and when a few inches apart flew at each other, met in mid-air, grappled, fell to the sand below, continued to wrestle for about a second or two, separated and both flew off. In another instance a female wasp was probing nest G when a second female flew toward G and the first female flew up and made contact with the intruder when the latter was approximately 2 inches from G. The argument might be made that females attacking other females are acting toward them as bee prey rather than territorial rivals. Reasons have already been cited making this most unlikely; one further reason involves the response of a female to a male which is nearly identical in appearance to the female. A male was on the mound of a nest which it had just closed, and it began flight. A female was engaged in hunting and was at the entrance of nest A. She spied the slow flying male and flew at the male but she did not hit him as she obviously would have done to a female; (but apparently recognized him as a male probably by chemical means) she continued to fly toward him but when approximately one inch from the male she broke off the pursuit without making contact.

Also recorded on 30 August were the number of aggressive attacks by one female at another or mutual attacks, the minimum of these were 26 between 2:06 AM and 5:26 PM with some large time lapses when the observer was not present or when his attention was directed in recording

other aspects of behavior. At 3:51 PM in about one 3-minute period, four aggressive female encounters occurred including chasing in the air, pouncing on the ground, and several wrestlings. So much female-female aggressive behavior occurred in that brief span because as many as four females were hunting at the same time in the small area of the vertical bank. At 4:06 PM much the same occurred, four females were hunting at the same time (at 4:12 PM five females were hunting at the same time and at 4:34 PM six females were similarly engaged), and I believe I observed greater hunting activity than I ever saw at any other time and also far more female aggressiveness than ever before. I didn't even record the number of encounters but certainly there were in that space of minutes at least five and probably closer to eight. I believe that during this time of day the highest frequency of hunting behavior and female *P. gibbosus* territorial aggressive behavior occurs. This might in fact be what is to be anticipated since it is probably the time when the bees return to their nest for the day after gathering pollen; it is also the time of day that the territorial females of *Philanthus gibbosus* "wait" for them around their favorite bee nests in their territories.

One medium or medium large female was marked with paint on 4 September. This was female 2. Female 2 was observed almost daily from 4-14 September in the vicinity of her hunting territory where she particularly localized around bee nest H which she often sat next to or attacked the guards in the entrance or pursued some passing bee in flight to or from the nest. She vigorously defended a territory about 2 square feet encompassing this area.

Discussion

Long term studies of *P. gibbosus* have revealed that 1972 was a year of exceedingly large populations of these wasps in Brooklyn. Halictine bees were also extremely common during that year. While untrue in other years, the major source of halictid bee mortality in the Brooklyn areas studied was due to the predation of *P. gibbosus* (for a comparison of the causes of halictine bee mortality in previous years in Brooklyn see Lin, 1964 and 1964-65). Hunting territories among *P. gibbosus* females was never observed in the large 40 acre field in Brooklyn (1956-1976) where years of data were gathered but was observed in the crowded conditions in a vertical bank in 1972 also in Brooklyn where both wasps and an unidentified species of halictine bee nested in large numbers.

Hunting territories probably arise under conditions of dense *P. gibbosus* populations when they are located in banks which also house the nests of halictine bees. A safe prediction is that such territories do not exist in large fields where intensive observation over the years has failed to re-

veal any female-female aggression other than that associated with encroachment by one female of another female's nest where prey species of bees are probably taken at flowers or dispersed nests. In years when *P. gibbosus* is scarce, hunting territories are probably nonexistent over banks inhabited by both wasps and halictine bees, especially should the latter be in excessive amount. This may be the explanation for the findings of Barrows and Snyder (1973) that *Lasioglossum zephyrum* was abundant in the nesting banks of *Philanthus gibbosus* and that the wasps apparently did not hunt near their nest which suggested that competition for prey was not great. Only prey shortage or predator abundance or both under these conditions may elicit territorial behavior.

Hunting territories in other digger wasps are here postulated to be uncommon due to the transitory nature of the location of their food supply as opposed to a rigidly fixed source in *Philanthus* provided by the permanent bee nests located in a small concentrated area of a bank or elsewhere in the current case.

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